THE DROUGHT AND POST-DROUGHT ABUNDANCE AND HABITAT DISTRIBUTION OF SMALL MAMMAL SPECIES IN BURNED AND UNBURNED, RESTORED TALLGRASS PRAIRIE

Peter Schramm
Department of Biology, Knox College, Galesburg, Illinois 61401, U.S.A.

David B. Dunn
U.S. Fish and Wildlife Service, North Central Experiment Station, Star Route 1, Box 7200, Ely, Minnesota 55731, U.S.A.

and

Linda Nachowicz
7219 West Lee Street, Niles, Illinois 60648, U.S.A.

Abstract. Drought and post-drought abundance and habitat distributions of small mammal species were monitored on burned and unburned, restored tallgrass prairie at the Knox College Biological Field Station, located in Knox County in west-central Illinois. Trap, mark, and recapture data were collected from October 1988 to March 1990. The prairie deer mouse (*Peromyscus maniculatus*), normally present in modest numbers, emerged as the dominant species during the drought and post-drought periods. Vole (*Microtus*) species, usually present in greater numbers, were absent during the drought and rare in the post-drought period. The prairie vole (*M. ochrogaster*) slowly re-established populations; the meadow vole *M. pennsylvanicus*) was scarce throughout the study. The white-footed mouse (*P. leucopus*) invaded the burned grid in low numbers in close proximity to the forest edge. The western harvest mouse (*Reithrodontomys megalotis*), extremely rare in previous studies, was absent during the drought but showed a high frequency of occurrence in the post-drought period. The continued low numbers of most of the small mammal species suggest that the effects of severe drought are long lasting. A new finding of this study indicates prairie deer mice avoid areas dominated by the allelopathic downy sunflower (*Helianthus mollis* Lam.). Adaptation to dryer conditions and absence of voles are suspected as the underlying causes of prairie deer mouse abundance.

INTRODUCTION

As part of an on-going, long-term study of small mammals in restored prairies, drought and post-drought abundance of small mammal species was monitored on burned and unburned, restored tallgrass prairie at Knox College's Biological Field Station. During the severe summer drought of 1988, prairie plants, particularly the grasses, were reduced to 25% of the height usually attained during summers of normal rainfall. Plant growth and seed production in all the grasses and some of the more shallowly rooted forbs were severely reduced although the more deeply rooted forbs, such as some of the silphiums and prairie legumes, were not significantly affected. The summer of 1989 brought increased precipitation, but the drought-affected plants returned to only 75% of their characteristic height during non-drought summers, and seed production was still negatively affected in the same species. The effects of this drought had a profound effect on the small mammal composition in this restored prairie.

The relationship between prairie habitat and the small mammals inhabiting it is dynamic, with vegetational physiognomy being a major cause of changes in species diversity, abundance, and distribution (Huntley and Inouye 1987). Precipitation has a major influence on the amount of vegetation growth and seed production (Krebs 1985). Moisture is also critical in determining the microhabitats of the prairie, which, in turn, can alter small mammal occurrence. Certain species, such as the meadow vole (*Microtus pennsylvanicus*) and shrews (*Sorex* and *Blarina*), have been shown to prefer moist conditions (Blackburn 1988, Getz 1961, Getz et al. 1987, Gottschang 1965, Synder and Best 1988). Others, like the prairie vole (*Microtus ochcrogaster*), tend to predominate in dryer areas (Getz 1961, Miller 1969, Schramm and Willcutts 1983).

Fire is also an important element in the development, maintenance, and seasonal productivity of grassland ecosystems (Anderson 1982). Fires occurred commonly during presettlement and are now used by managers to maintain the prairie community and halt the encroachment of forest, woody shrubs, and non-native herbaceous weeds. Frequent fires amplify herbage and flowering-stalk production (Hadley and Kieckhefer 1963) while decreasing litter accumulation (Hulbert 1969). Burned and unburned prairie communities contain uniquely different microhabitats. The accumulation of litter in unburned prairie forms a protective barrier at ground level that increases the relative humidity (Hulbert 1969) and provides shelter for some small mammals. The absence of litter on the burned prairie decreases topsoil moisture levels (Hulbert 1969), increases seed availability, increases exposure of small mammals to predators and environmental conditions, and leaves a litter-free understory later in the growing season (Kaufman et al. 1988). Studies have shown that voles (*Microtus* sp.) commonly inhabit areas of dense growth and litter cover (M'Closkey and Fieldwick 1975, Schramm 1970, Schramm and Willcutts 1983, Vacanti and Geluso 1985, Synder and Best 1988), but meadow jumping mice (*Zapus hudsonius*), prairie deer mice (*Peromyscus maniculatus*), and white-footed mice (*Peromyscus leucopus*) prefer more open areas with reduced litter (Schramm 1970, Schramm and Willcutts 1983, and Kaufman et al. 1988). Because of the infrequency of drought, however, no study has been able to document the effect on small mammal occurrence of extreme drought coupled with burning or litter accumulation. The purpose of this study was to investigate this effect.

MATERIALS AND METHODS

Study Area

This study was conducted from October 1988 to March 1990 at the Knox College Biological Field Station, in Knox County in west-central Illinois, on three 0.16-ha plots (grids) of restored tallgrass prairie (Figure 1). Burned Grid I was burned in March of 1987, 1988, and 1989, resulting in the absence of standing dead plants and plant litter on this plot. Intermediate Grid II was burned in March 1987 and 1988, resulting in moderate amounts of litter accumulation and standing dead plant material present on this grid during the post-drought period. Unburned Grid III had not been burned since March 1986 and contained an extremely heavy accumulation of litter and standing dead plant material at ground level throughout the study. Predominant vegetation on Burned Grid I consisted of big bluestem (*Andropogon gerardi* Vitm.), Indian grass (*Sorghastrum nutans* Nash.), yellow sweet clover (*Melilotus officinalis* Lam.), and white sweet clover (*Melilotus alba* Desr.). Intermediate Grid II was dominated by big bluestem, Indian grass, switch grass (*Panicum virgatum* L.), and downy sunflower (*Helianthus mollis* Lam.). Unburned Grid III was primarily covered by a mixture of big bluestem and Indian grass. Prairie forbs occurring on all the grids included purple and white prairie clover (*Petalostemum purpureum* Rydb. and *P. candidum* Michx.), lead plant (*Amorpha canescens* Pursh), white false indigo (*Baptisia leucantha* T. & G.), showy tick trefoil (*Desmodium canadense* DC.), round-headed bush clover (*Lespedeza capitata* Michx.), compass plant (*Silphium laciniatum* L.), prairie dock (*Silphium terebinthinaceum* Jacq.), stiff goldenrod (*Solidago rigida* L.), old field goldenrod (*Solidago nemoralis* Ait.), pale purple cone flower (*Echinacea pallida* Nutt.), wild quinine (*Parthenium integrifolium* L.), rattlesnake master (*Eryngium yuccifolium* Michx.), mountain mint (*Pycnanthemum virginianum* Dur. & Jacks.), culvers root (*Veronicastrum virginicum* Farw.), spiderwort (*Tradescantia ohiensis* Raf.), and yellow gentian (*Gentiana flavida* A. Gray).

Trapping Procedures

Each grid was a 40 by 40 meter square with Sherman live-traps placed at 10 meter intervals, resulting in 25 trapping stations per grid. Traps were set for four consecutive nights. Each trapping session consisted of four nights of trapping followed by a six night non-trapping interval. Between each session, all traps were removed. Trapping/non-trapping intervals were continual from 17 October 1988 to 5 March 1990, resulting in 32 trapping periods, for a total of 7200 trapnights. Traps were baited with commercial bird seed and checked daily. During winter months, traps were baited with one part peanut butter and one part vegetable oil combined with bird seed mix to provide additional calories for cold-weather survival. A ball of cotton for bedding was also placed in each trap. Upon capture, each animal was marked with a small, numbered, aluminum ear tag, and the following parameters were recorded: trapping period, date, tag number, grid, station number, species, sex, age, reproductive condition, weight, and any distinguishing characteristics.

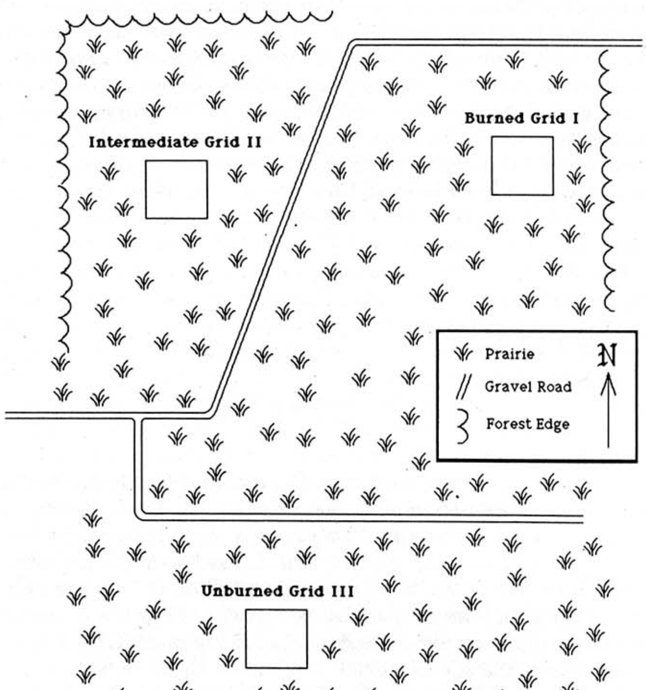

Figure 1. Map of the study area showing locations and habitats of the burned, intermediate, and unburned trapping grids.

Analysis of Data

The total number of each species in each grid was calculated. An animal was considered present or in the near vicinity in all periods between its first and last capture. Small grid size, time between recaptures, and absence of capture on theother grids of this limited habitat contributed to this conclusion. Chi-square analysis was used to determine significant differences in populations between grids and species. Pearson r and variance (R2) were also used to measure significance. Populations of individual species were measured over time.

RESULTS

Abundance and Species Composition

In this study, 301 individuals, representing nine species of small mammals, were captured 1,086 times (Table 1). The species present, in decreasing order of abundance, were prairie deer mouse (*Peromyscus maniculatus*), prairie vole (*Microtus ochrogaster*), masked shrew (*Sorex cinereus*), western harvest mouse (*Reithrodontomys megalotis*), short-tailed shrew (*Blarina brevicauda*), white-footed mouse (*Peromyscus leucopus*), house mouse (*Mus musculus*), meadow jumping mouse (*Zapus hudsonius*), and meadow vole (*Microtus pennsylvanicus*). Prairie deer mice accounted for 60.8% of the total individuals and 75.5% of the total captures. Prairie voles accounted for 11.3% of the total individuals and 4.0% of the total captures. The masked shrew accounted for 10% of the total individuals and 3.6% of the total captures. The western harvest mice accounted for 7.3% of the total individuals and 7.7% of the total captures. The remaining 10.6% of the total individuals and 9.2% of the total captures were distributed among the other 5 species encountered.

During the drought, prairie deer mice were present in significantly greater numbers on both the burned grid and the unburned grid than were other small mammal species (Figures 3 and 5). Voles, jumping mice, harvest mice, and shrews were completely absent from all grids during the drought but re-established themselves in low numbers during the post-drought period. White-footed mice were present in low numbers during the drought on the burned grid, and house mice were captured occasionally throughout the study. Prairie deer mice continued to dominate in numbers during the post-drought response on the burned and unburned grids. Prairie deer mice, along with prairie voles, harvest mice, and shrews, appeared late in the post-drought period on the intermediate grid (Figure 4). There were no marked differences in populations among any small mammal species on the intermediate grid.

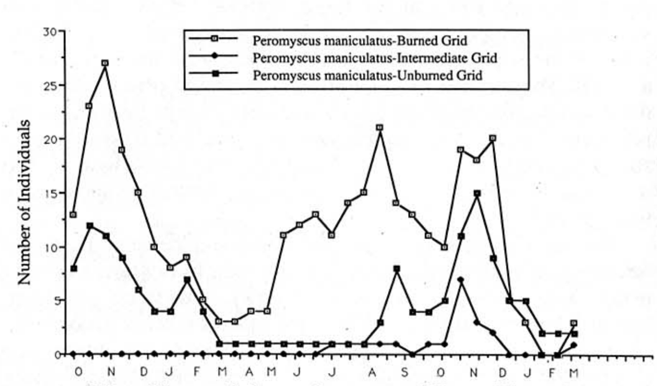

Figure 2. Comparison of *Peromyscus maniculatus* numbers on all grids through time.

Habitat Preferences and Distribution of *Peromyscus* Species

Prairie deer mice were present on all grids but occurred in the highest numbers on the burned grid (Figure 2). Populations on the burned grid were three times greater than those on the unburned grid and were significantly greater than those of the unburned and intermediate grids (X2=142.67, d.f.=2, P=<.01). Maximum population peaks occurred in late summer and fall, perhaps related to a time of maximum seed availability. No distinct differences occurred in abundance between the unburned grid and the intermediate grid (X^2=0.029, d.f.=1, P=<.01). Overall abundances of prairie deer mice declined in each grid during the post-drought period.

White-footed mice occurred only in the burned grid, primarily along the eastern boundary in close proximity to the forest edge.

Effects of the Downy Sunflower, *Helianthus mollis* Lam.

Capture points for prairie deer mice on the intermediate grid indicated a general avoidance of areas dominated by the downy sunflower (Figure 6). The two animals captured in this area were juveniles, captured late in the growing season.

Habitat Distribution of *Microtus* Species

The absence of prairie voles and meadow voles suggests significant differences in habitat preference and drought adaptability. Prairie voles were not captured until May 1989, 9 months after the severe summer drought (Figures 3 and 4). There were no significant differences between populations on any grid (X2=4.67, d.f=2, P=<.05), but a negative relationship appeared between litter accumulation and population densities, with the greatest number of prairie voles occurring on the burned grid. This species increased significantly during the post-drought period on the burned prairie (r=.6935, d.f.=12, P=<.01), moderately on the unburned prairie (r=.2191, d.f.=5, P = <.05, Figure5), and there was apparent population crash on the intermediate prairie, with numbers decreasing significantly over time (r=.6557, d.f.=15, P=<.01).

Meadow vole populations were severely reduced during the drought. There were only two meadow voles captured during the entire trapping period, both occurring 19 months after the drought. Both captures occurred on the unburned grid, where the greatest accumulation of litter was present.

Habitat Distribution of *Reithrodontomys* and Other Species

Western harvest mice were not captured during the drought, but numbers significantly increased during the post-drought period on the burned (r=-.6935, d.f.=6, P=<.05) and intermediate grids (r=.6215, d.f.=6, P=<.05, Figures 3 and 4). There were no significant differences in numbers between these grids (X2=0.0909, d.f.=2, P=<.05), but harvest mice did seem to prefer the burned and intermediate plots over the unburned plot (Figure 5).

Masked shrews and short-tailed shrews were not found during the drought but substantially increased in abundance during the post-drought period. Masked shrews first appeared 11 months after the drought summer and were present in all grids. Short-tailed shrews appeared 13 months after the drought summer but remained in very low numbers. Masked shrews outnumbered short-tailed shrews on each grid by a two to one ratio. There appeared to be a relationship between shrew populations and litter cover, with both species having the greatest densities on the unburned and intermediate grids and the lowest densities on the burned grid.

Meadow jumping mice and house mice were rare species during the study; however, house mice were caught in very low numbers on the burned and unburned grids during the drought.

DISCUSSION

The most striking effect of the severe summer drought of 1988 was the sharp reduction of total small mammal numbers and species diversity in all the habitats of the restored prairie. Past studies of the Knox College Field Station prairie in nondrought years found abundant populations of voles and shrews and the presence of jumping mice and harvest mice (Schramm 1970, Springer and Schramm 1972, Moreth and Schramm 1973, Schramm and Willcutts 1983). However, a deficit of more than 12 inches of rain in the summer of 1988 (National Oceanic and Atmospheric Administration, 1988) severely reduced the dominant prairie grass productivity and greatly altered the plant physiognomy and microhabitat, thus, changing the species of small mammals present, their numbers, and their distributions.

Effects of Drought on *Peromyscus* Species

The prairie deer mouse was the dominant species on the burned and unburned prairie during the drought. Past studies conducted on this prairie in nondrought years found modest numbers of prairie deer mice, abundant populations of voles, and the presence of as many as six other speices of small mammals (Schramm and Willcutts 1983, Moreth and Schramm 1973). However, during the extremely dry conditions of 1988, vole species, harvest mice, shrew species, and jumping mice did not occur at all on the prairie. During the drought, deer mice colonized areas and attained high densities uncharacteristic of nondrought years. Grant (1971) demonstrated that removal of voles alone could cause deer mice populations to increase. The absence of harvest mice and shrews might also play a role in the increase of deer mice numbers. Kaufman et al. (1988) found a negative relationship between high populations of deer mice and harvest mice, suggesting a possible competitive relation-

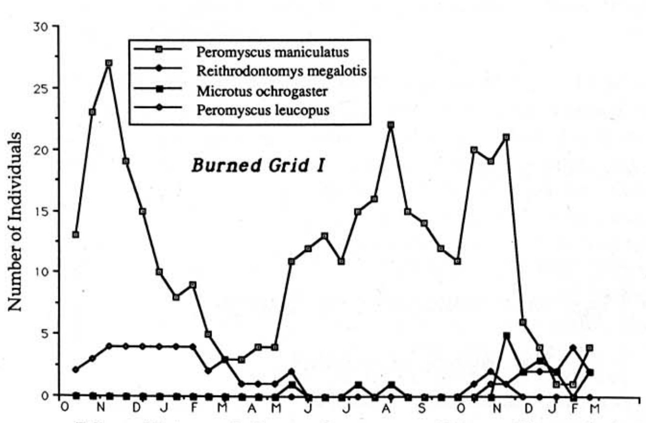

Figure 3. Comparison of mammal species numbers through time on Burned Grid I.

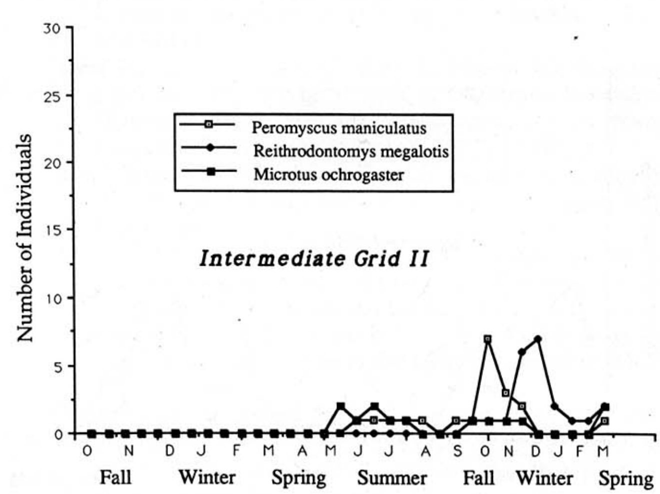

Figure 4. Comparison of mammal species numbers through time on Intermediate Grid II.

ship, but concluded habitat differences played a critical role. Short-tailed shrews have been documented as negatively affecting deer mice populations (Blackburn 1988).

That prairie deer mice have a preference for burned prairie over unburned prairie has been well documented (Schramm and Willcutts 1983, Moreth and Schramm 1973, Kaufman et al. 1988). Deer mice are primarily seed eaters and move in a series of short leaps and quick changes in direction (Gambaryan 1974). Litter accumulation on unburned prairie alters seed availability (Kaufman et al. 1988) and ease of movement, thus increasing foraging time, vulnerability to predators, and energy expenditure while moving about during above-ground activity (Schramm and Willcutts 1983). This study also found a positive association between deer mice populations and burned prairie. However, deer mice were also the dominant species on the unburned grid during all trapping periods. This differs distinctly from previous studies in this prairie during years with normal precipitation and strongly suggests that the drought, by greatly reducing the presence of other small mammal species, allowed the prairie deer mouse, in the absence of the usual interspecific competition, to colonize areas not normally used and to attain densities not possible during nondrought years.

Effects of Drought on *Microtus* Species

Vole species were completely absent during the drought and were found in reduced numbers during the post-drought period. Prairie voles were present on all grids during the post-drought period but were more prevalent in burned areas of reduced litter cover. This agrees with some studies that have shown that prairie voles prefer dry upland areas (Getz 1961) and, unlike meadow voles, can, in some years, show an affinity for burned prairie as well (Schramm and Willcutts 1983).

Meadow voles occurred very late in the post-drought period and were extremely rare. The importance of meadow voles in mesic grassland communities has been widely documented (Synder and Best 1988, Schramm 1970, Schramm and Willcutts 1983, Vacanti and Geluso 1985). Meadow voles are positively associated with heavy litter cover and very moist conditions (Getz 1961, Schramm 1970, Schramm and Willcutts 1983, Moreth and Schramm 1973, Synder and Best 1988). Miller (1969) described meadow voles as primarily lowland species, and Risser et al. (1981), described the meadow vole as an ecotonal species inhabiting the forest edge community. These findings point to the importance of moisture for this species. The effects of the drought were long lasting on meadow vole populations in the Knox prairie.

Typically, voles are slower in reestablishing populations after fire than are other small mammals. Meadow vole density is positively correlated with thickness of vegetational cover and increased litter accumulation (Vacanti and Geluso 1985). This species may take 12-16 months after a burn to repopulate areas to preburn densities (Vacanti and Geluso 1985) or may not even recover original numbers in more than 24 months (Schramm 1970). The prairie vole is more variable; Schramm and Willcutts (1983) clearly demonstrated differential response of the prairie vole compared to the meadow vole in burned and unburned prairie plots. During some years, the prairie vole can invade recently burned prairie and expand rapidly. At the same time, it may be partially excluded from adjoining unburned prairie by the presence of a lower but well-established population of meadow voles (Schramm and Willcutts 1983). In the current study, drought and fire combined to eliminate all voles on the burned grid and intermediate grid and drought alone had the same total elimination effect on both species on the unburned grid.

It should be noted that in 26 years of on-going observations and periodic trapping of voles in the restored prairies of the Knox field station, no classic, short-term, periodic, three to four year cycles have been observed, even in the less frequently burned portions of this habitat. Other recent studies in warm-season native-grass plots seem to agree on this point (Getz et al. 1987, Meserve and Klatt 1985).

Effects of Drought on *Reithrodontomys* and Other Species

One of the more unusual composition changes during the post-drought response was the relative increase in populations of the western harvest mouse. Kaufman et al. (1988) found that western harvest mice prefer areas of intermediate litter cover but will reside in both burned prairies, especially during high seed density, and unburned prairies. Western harvest mice nest above ground and may be affected by frequent fires. However, some studies show an increase in harvest mice density after fire (Vacanti and Geluso 1985). Although harvest mice are usually present in relatively low numbers (Kaufman et al. 1988), we found nearly twice the number of individuals as were found on the same prairie in nondrought years (Schramm and Willcutts, 1983). Although Kaufman et al.

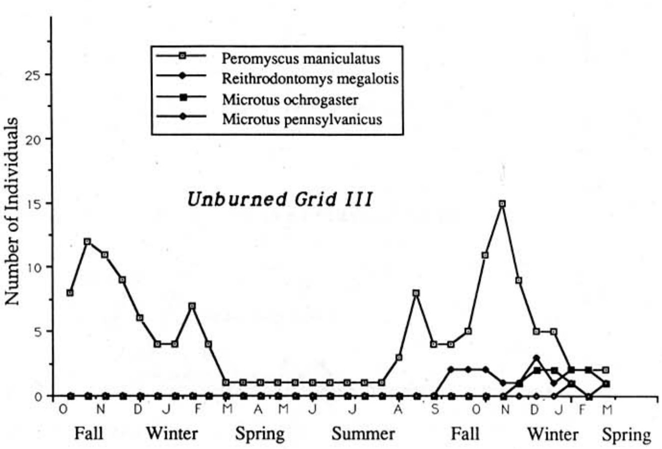

Figure 5. Comparison of mammal species numbers through time on Unburned Grid III.

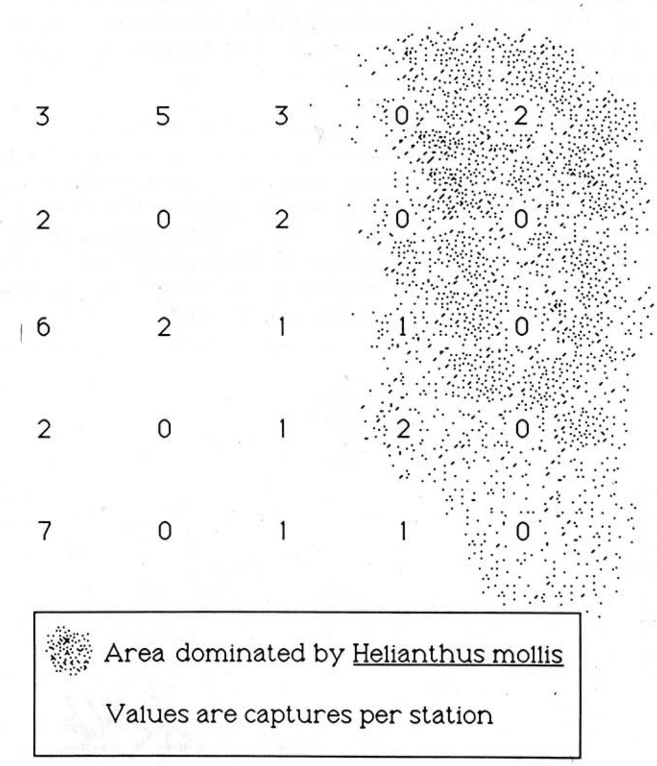

Figure 6. Captures points of *Peromyscus maniculatus* on Intermediate Grid II in relation to the allelopathic downy sunflower, *Helianthus mollis*.

Table 1. Total number of individuals for all species on each grid.

Species	*Burned Grid I*	*Intermediate Grid II*	*Unburned Grid III*	*Totals*
Peromyscus maniculatus	124	17	42	183
Microtus ochrogaster	17	10	7	34
Sorex cinereus	5	15	10	30
Reithrodontomys megalotis	7	8	7	22
Blarina brevicauda	1	7	4	12
Peromyscus leucopus	11	0	0	11
Mus musculus	2	2	1	5
Zapus hudsonius	1	1	0	2
Microtus pennsylvanicus	0	0	2	2
Totals	168	60	73	301

(1988) found a possible competitive relationship between deer mice and harvest mice, differences in habitat were cited as more important than possible interspecific competition. In our study, a more critical factor may have been the total absence of voles. Heske et al. (1984) demonstrated that interspecific competition did exist between voles and harvest mice, even though voles are primarily herbivorous and harvest mice omnivorous. The effect of the drought in eliminating the voles may have assisted harvest mice in achieving above-normal densities.

White-footed mice were found along the eastern portion of Burned Grid I. This agrees with other studies that found white-footed mice are natural forest-prairie edge dwellers and readily take to the pairie for nightly foraging (Schramm and Willcutts 1983, Clark et al. 1987, Synder and Best 1988, Kantak 1983). Although white-footed mice did increase during the post-drought period, no significant differences were found in their prairie use between drought and post-drought periods.

Shrews were absent during the drought but returned during the post-drought period. Masked and short-tailed shrews are regular residents of the tallgrass prairie (Schramm 1970, Springer and Schramm 1972, Moreth and Schramm 1973, Synder and Best 1988, Schramm and Willcutts 1983). Short-tailed shrews are recognized as a ubiquitous species, inhabiting all types of habitat, with vegetational cover having little influence on their distribution (Blackburn 1988). Masked shrews have been reported in many habitats but do not seem to be as widespread as short-tailed shrews (Blackburn 1988, Synder and Best 1988). Masked shrews increased significantly during the post-drought period, becoming the third most abundant species on the prairie. Short-tailed shrews were slower to recover and remained in low numbers. Although both species could be found in xeric habitats, they seemed to prefer more mesic sites in this study (Table 1).

Effects of Downy Sunflower on Distrbution of Prairie Deer Mice

Recent studies have focused on effects of plant chemical defenses on small mammals (Lindroth and Batzli 1986, Lindroth et al. 1986). Many plants produce phenolics in response to grazing and as a competitive defense in warding off the intrusion of other plant species. The highly allelopathic downy sunflower (*Helianthus mollis*) is found in successional stages and disturbance sites of tallgrass prairie. A stand of this sunflower is present along the eastern portion of Intermediate Grid II. During the post-drought period, captures per trap site indicated that deer mice were avoiding this area (Figure 6). The only captures in this area were two juveniles trapped late in the growing season. Lindroth et al. (1986) found that phenolics can cut the absorption of plant proteins by one half in voles but were unclear as to how this affected wild populations. The presence of this sunflower in the Knox prairies greatly reduces the presence of other prairie plants, both grasses and forbs, and this, in turn, may affect the presence of deer mice. Investigation of this phenomenon is continuing.

CONCLUSIONS

Few studies have followed the effects of severe summer drought and post-drought changes on small mammal species diversity, relative population densities, and distributions in burned and unburned prairies. During the drought, not only was plant growth greatly reduced, but small mammal populations and diversity declined as well. Both burned and unburned prairie communities were greatly affected by the drought. In the post-drought period, population density and species diversity gradually increased. Small mammal population density continued to be greater in burned areas while unburned areas with more litter cover appeared to be slower in recovering numbers and species diversity. The dominance of prairie deer mice in burned and unburned plots and the unusually high frequency of occurrence of western harvest mice suggest the importance of voles in influencing small mammal distribution and abundance in the prairie. With the reappearance of voles and shrews after the drought, the dominance by prairie deer mice appeared to be changing. Normally abundant species, such as voles, were severely affected by the drought but had started a slow recovery in numbers. Prairie voles were faster in their recovery than meadow voles, which continued to be rare. It is apparent that the effects of the drought were persisting well into the year after the drought, and the small mammal populations were still being affected residually by this phenomenon. Study is continuing as the Knox prairie recovers from the severe drought of 1988.

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